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Studies on the genetic basis of heterosis and inbreeding depression for seed yield and its component traits in castor (*Ricinus communis* L.)

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Abstract

The present investigation was undertaken with a view to generate genetic information on heterosis and inbreeding depression for seed yield and its component traits. The heterosis over better parent was found significant in desirable direction for total length of primary raceme, effective length of primary raceme, shelling out turn, 100-seed weight and seed yield per plant in JM-6 x 48-1 and for days to maturity of primary raceme, plant height up to primary raceme, number of nodes up to primary raceme, number of capsules on primary raceme, shelling out turn and oil content in JI-436 x PCS-124. Significant and positive inbreeding depression was observed for number of nodes up to primary raceme, total length of primary raceme, effective length of primary raceme, number of capsules on primary raceme, 100-seed weight, seed yield per plant and oil content in JM-6 x 48-1 and for days to maturity of primary raceme, number of effective branches per plant, number of capsules on primary raceme and oil content in JI-436 x PCS-124. The observed and expected estimates for relative heterosis, heterobeltiosis and inbreeding depression were in close agreement with either expected (1) or expected (2) for seed yield per plant and its component traits in both crosses of castor.

Keywords: Heterosis, inbreeding depression, gene effects, 21 generations

Introduction

Exploitation of hybrid vigour in castor has been recognized as a practical tool in providing the plant breeders a mean for improving seed yield and other important traits, which became feasible due to availability of 100% pistillate lines (Gopani *et al.,* 1968). On the other hand, the inbreeding depression reflects through the reduction in vigour. Commercial exploitation of heterosis in castor is regarded as the major breakthrough in the field of castor improvement since the release of first castor hybrid GCH 3 in Gujarat during 1968. Since then, nine other castor hybrids *viz*., GAUCH 1, GCH 2, GCH 4, GCH 5, GCH 6, GCH 7, GCH 8, GCH 9 and GCH 10 were released subsequently covering nearly 90 per cent of the total area under castor cultivation in Gujarat. The study of nature and magnitude of heterosis is useful in identifying superior cross combinations and its exploration to get better transgressive segregates. Moreover, the study of heterosis *vis-a-vis* analysis of genetic effects provides understanding of genetic basis of observed heterosis. Gene system is useful to compare observed heterosis and inbreeding depression with expected ones.

Materials and Methods

The basic set of twenty-one generations *viz*., P_1, P_2, F_1, F_2, F_3, B_1 (F_1 x P_1), B_2 (F_1 x P_2), B_{11} (B_1 x P_1), B_{12} (B_1 x P_2), B_{21} (B_2 x P_1), B_{22} (B_2 x P_2), B_{1S}, B_{2S}, B_1 x F_1, B_2 x F_1, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip and F_2 bip, derived from two crosses namely JM-6 x 48-1 (cross 1) and JI-436 x PCS-124 (cross 2) were sown in Compact Family Block Design with three replications during *kharif* 2020-21. The plots of various generations contained different number of rows *i.e*., parents and F_1 in single row; B_1 and B_2 in two rows and F_2, F_3, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, B_1 x F_1, B_2 x F_1, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip and F_2 bip in four rows. Each row was of 6 m in length with 120 cm and 60 cm inter and intra row spacing, respectively. All the recommended agronomical practices and necessary plant protection measures were followed timely to raise good crop of castor. The observations were recorded on five competitive and randomly selected plants from P_1, P_2 and F_1; ten plants from backcross (B_1 and B_2) and twenty plants from F_2, F_3, B_{11}, B_{12}, B_{21}, B_{22}, B_{1S}, B_{2S}, B_1 x F_1, B_2 x F_1, F_2 x P_1, F_2 x P_2, F_2 x F_1, B_1 bip, B_2 bip and F_2 bip generations in each replication for twelve traits.

The heterotic effects in term of superiority of F_1 over better parent (heterobeltiosis) as per Fonseca and Patterson (1968) [7]; over mid parent value (relative heterosis) as per Briggle (1963) [4]; and inbreeding depression as per Allard (1960) [2] was worked out as loss in vigour due to inbreeding and difference between mean of F_1 and F_2. The expected heterosis and inbreeding depression for different characters were calculated as under (Based on formulae given by Mather and Jinks, 1982) [12].

(A) The expected heterosis and inbreeding depression for different characters, where simple additive-dominance model was adequate, were calculated as,

1) Heterosis over better parent

(i) $F_1 - P_1 = [h] - [d]$

(ii) $F_1 - P_2 = [h] - [-d]$

2) Heterosis over mid parent = $[h]$

3) Inbreeding depression = $[h]/2$

(B) For the characters where the digenic interaction model was found adequate, the expected heterosis and inbreeding depression were determined using the parameters of best fitting model. For example, the expectation of heterosis and inbreeding depression measured on a six parameters scale had the following form,

1) Heterosis over better parent

(i) $F_1 - P_1 = ([h] + [1]) - ([d] + [i])$

(ii) $F_1 - P_2 = ([h] + [1]) - (-[d] + [i])$

2) Heterosis over mid parent = $([h] + [1]) - [i]$

3) Inbreeding depression = $(1/2)\,[h] + (3/4)\,[l]$

(C) For the characters where the trigenic interaction model was found adequate, the expected heterosis and inbreeding depression were calculated as under:

1) Heterosis over better parent

(i) $F_1 - P_1 = ([h] + [l] + [z]) - ([d] + [i] + [w])$

(ii) $F_1 - P_2 = ([h] + [l] + [z]) - ([-d] + [i] - [w])$

2) Heterosis over mid parent = $([h] + [l] + [z]) - [i]$

3) Inbreeding depression= $(1/2)\,[h] + (3/4)\,[l] + (7/8)\,[z]$

(D) Linkage does not affect the means of non-segregating generations (P_1, P_2 and F_1) irrespective of the absence or presence of epistasis and is thus unable to bring any change in the specification of heterosis. However, it is able to cause bias in the estimates of [h], [i] and [l] as well as [w] and [z] components and misrepresent the relative importance of these components in the manifestation of heterosis. As a result, the interpretation about the cause of heterosis is also changes. Where, (d) = Additive gene effect, (h) = Dominance gene effect, (i) = Additive x additive gene effect, (j) = Additive x dominance gene effect, (l) = Dominance x dominance gene effect, (w) = Additive x additive x additive gene effect, (x) = Additive x additive x dominance gene effect, (y) = Additive x dominance x dominance gene effect and (z) = Dominance x dominance x dominance gene effect.

Results and Discussion

The perusal of results presented in Table 1 indicated that the extent of heterosis over mid parent and better parents was not pronounced for various characters recorded in two crosses. For the characters like days to flowering of primary raceme, days to maturity of primary raceme, plant height up to primary raceme and number of nodes up to primary raceme, the low scoring parent was taken as better parent. The heterosis over better parent was significant and negative for early maturity in cross JI-436 x PCS-124. The heterosis over better parent was significant and positive for days to flowering of primary raceme and days to maturity of primary raceme in cross JM-6 x 48-1 indicated delay in flowering and maturity in this hybrid combination. The heterosis over better parent was significant and negative for dwarf stature in cross JI-436 x PCS-124. The heterosis over better parent was significant and positive for tall plant height in cross namely, JM-6 x 48-1. Similarly, for lesser number of nodes up to primary raceme the cross, JI-436 x PCS-124 manifested significant and negative heterobeltiosis, while significant and positive heterobeltiosis for more number of nodes up to primary raceme was recorded in cross, JM-6 x 48-1. The heterosis over better parent was significant and positive for longer length of primary raceme and effective length of primary raceme in cross JM-6 x 48-1 and significant and negative for shorter length of primary raceme and effective length of primary raceme in cross JI-436 x PCS-124. The heterosis over better parent was significant and negative for lesser number of effective branches per plant in the both crosses, JM-6 x 48-1 and JI-436 x PCS-124. The heterosis over better parent was significant and positive for more number of capsules on primary raceme in cross JI-436 x PCS-124 and significant and negative for lower number of capsules on primary raceme in cross JM-6 x 48-1. The heterosis over better parent was significant and positive for higher shelling out turn in both the crosses, JM-6 x 48-1 and JI-436 x PCS-124. The heterosis over better parent was significant and positive for higher test weight in cross, JM-6 x 48-1. The heterobeltiosis was significant and positive for higher seed yield per plant in cross, JM-6 x 48-1 and significant and negative for lower seed yield per plant in cross JI-436 x PCS-124, while it was significant and positive in cross JI-436 x PCS-124 for high oil content.

Table 1: Estimates of observed and expected heterosis and inbreeding depression for twelve characters in two crosses of castor

Heterosis/ Inbreeding depression	Observed/ Expected values	Days to flowering of primary raceme	Days to maturity of primary raceme	Plant height up to primary raceme (cm)	Number of node up to primary raceme	Total length of primary raceme (cm)	Effective length of primary raceme (cm)	Number of effective branches per plant	Number of capsules on primary raceme	Shelling out turn (%)	100-seed weight (g)	Seed yield per plant (g)	Oil content (%)
JM-6 x 48-1 (cross 1)													
Mid parent	Observed	-12.53** ±0.94	-3.77* ±1.68	5.23** ±1.32	1.43** ±0.41	19.67** ±1.74	20.47** ±1.91	-0.83** ±0.27	-1.27 ±2.64	3.45** ±0.52	3.23** ±0.34	60.80** ±8.52	0.36** ±0.13
	Expected (1)	-13.30	-2.72	5.30	1.36	19.53	20.22	-0.82	-2.16	3.64	3.16	51.21	0.31
	Expected (2)	-11.58	2.10	4.05	0.76	7.72	8.66	-0.72	-5.51	3.21	0.15	11.18	0.30
Better parent	Observed	11.93** ±1.03	29.00** ±1.57	9.87** ±1.27	3.00** ±0.47	4.73* ±1.95	4.73* ±2.22	-3.13** ±0.36	-45.80** ±2.86	1.25* ±0.52	0.94* ±0.38	23.01* ±10.77	0.28 ±0.15
	Expected (1)	10.59	27.67	9.91	2.76	4.81	4.70	-3.09	-46.37	1.27	0.95	14.16	0.21
	Expected (2)	9.79	24.94	8.89	2.12	-2.42	-2.89	-2.34	-47.38	-0.33	-1.50	-24.15	0.28
Inbreeding depression	Observed	-6.18** ±2.02	-5.87* ±2.45	-3.47 ±2.01	1.88** ±0.42	22.93** ±2.68	25.72** ±2.76	-1.00** ±0.36	21.30** ±4.11	-1.56* ±0.66	2.07** ±0.39	36.31* ±14.04	0.49** ±0.15
	Expected (1)	0.29	-6.57	-1.17	1.65	12.16	14.61	0.54	10.73	-1.99	2.38	66.99	0.74
	Expected (2)	-4.25	-5.73	-3.82	1.36	9.86	12.44	-1.10	12.66	-3.14	0.92	-7.73	0.47
JI-436 x PCS-124 (cross 2)													
Mid parent	Observed	0.30 ±0.72	-4.90** ±1.11	-5.60** ±1.03	-0.40 ±0.27	-6.00** ±1.19	-5.80** ±1.23	-0.37 ±0.31	4.47** ±0.91	4.37** ±0.51	1.34** ±0.26	7.07** ±2.48	0.74** ±0.18
	Expected (1)	0.14	-5.00	-5.04	-0.50	-6.12	-6.00	-0.63	4.59	4.52	1.50	7.10	1.03
	Expected (2)	-0.97	-3.86	-3.33	-0.53	-3.70	-3.30	-1.23	2.99	3.57	1.29	3.22	0.38
Better parent	Observed	-1.40 ±0.83	-7.07** ±1.18	-7.13** ±1.42	-0.87* ±0.33	-8.87** ±1.22	-8.47** ±1.40	-1.47** ±0.36	2.87** ±0.92	1.70** ±0.60	-0.37 ±0.32	-10.36** ±3.05	0.68** ±0.24
	Expected (1)	-1.77	-7.33	-5.08	-0.83	-8.76	-8.27	-1.60	2.88	2.46	-0.10	-10.50	0.93
	Expected (2)	-3.53	-7.35	-3.39	-0.71	-5.86	-4.68	-1.94	2.56	2.16	0.17	-13.60	0.16
Inbreeding depression	Observed	0.08 ±0.96	4.25** ±1.50	-5.47** ±1.22	0.03 ±0.28	-1.30 ±1.49	-1.45 ±1.50	1.15** ±0.38	10.50** ±1.46	-0.93* ±0.42	-1.19** ±0.33	3.46 ±8.35	0.49** ±0.18
	Expected (1)	0.49	-3.70	-2.71	0.13	-1.36	-0.68	0.62	15.43	-2.82	0.28	-1.42	0.57
	Expected (2)	-1.31	2.94	-7.15	-0.18	0.34	0.71	0.28	12.33	-1.11	0.21	9.33	0.44

Expected (1) - Trigenic interaction model
Expected (2) - Linked digenic interaction model

The heterosis over mid parent was significant and negative for days to flowering of primary raceme in JM-6 x 48-1, while for days to maturity of primary raceme in crosses,

JM-6 x 48-1 and JI-436 x PCS-124, which indicated earliness in flowering and maturity in these hybrid combinations, respectively. The heterosis over mid parent was significant and positive for tall plant height in cross JM-6 x 48-1 and significant and negative for dwarf stature in cross JI-436 x PCS-124. The relative heterosis was significant and positive in cross JM-6 x 48-1 for number of nodes up to primary raceme. The heterosis over mid parent was significant and positive for total length of primary raceme and effective length of primary raceme in cross, JM-6 x 48-1 and significant and negative for total length of primary raceme and effective length of primary raceme in cross JI-436 x PCS-124. The heterosis over mid parent was significant and negative for number of effective branches per plant in cross JM-6 x 48-1. The relative heterosis was significant and positive in cross JI-436 x PCS-124 for number of capsules on primary raceme. The relative heterosis was significant and positive for shelling out turn, test weight, seed yield per plant and oil content in both the crosses, JM-6 x 48-1 and JI-436 x PCS-124.

As observed in present study, several research worker have also reported heterosis in desirable direction for days to flowering and days to maturity of primary raceme by Joshi *et al.* (2002), Lavanya and Chandramohan (2003) and Delvadiya *et al.* (2018) [9, 10, 5]; for plant height up to primary raceme by Patel *et al.* (2013) [15], Punewar *et al.* (2017) [19] and Movaliya (2020) [14]; for number of nodes up to primary raceme by Thakkar *et al.* (2005) [21], Punewar *et al.* (2017) [19], Aher *et al.* (2020) [1]; for length of primary raceme by Punewar *et al.* (2017) [19], Delvadiya *et al.* (2018) [5], Mori (2019) [13], Movaliya (2020) [14] and Aher *et al.* (2020) [1]; for number of capsules on primary raceme by Patted *et al.* (2016) [18], Punewar *et al.* (2017) [19], Delvadiya *et al.* (2018) [5]; for shelling out turn by Delvadiya *et al.* (2018) [5], Mori (2019) [13] and Movaliya (2020) [14]; for 100-seed weight by Punewar *et al.* (2017) [19], Mori (2019) [13] and Movaliya (2020) [14]; for seed yield per plant by Delvadiya *et al.* (2018) [5], Patel *et al.* (2018) [16], Dube *et al.* (2018) [6], Mori (2019) [13], Movaliya (2020) [14] and Aher *et al.* (2020) [1]; and for oil content by Lavanya and Chandramohan (2003) [10], Patel *et al.* (2013) [15], Punewar *et al.* (2017) [19], Mori (2019) [13] and Movaliya (2020) [14].

The characters like days to flowering of primary raceme, plant height up to primary raceme and number of nodes up to primary raceme are not directly related to seed yield per plant, but they are important in determining the maturity period. Usually short stature lines with less number of nodes up to primary raceme, matures earlier than the taller line with high number of nodes. Thus, from the viewpoint of developing early maturing and short stature varieties / hybrids, the trend of negative heterosis for plant height up to primary raceme and number of nodes up to primary raceme is most desirable and essential feature, which should be exploited in term of negative heterosis. In the present study, cross JI-436 x PCS-124 possessed significant and negative mid-parent as well as better parent heterosis for plant height up to primary raceme and could be exploited for the development of short stature hybrids.

The observed heterosis over mid parent and better parent either significant or non-significant showed a close agreement to expected (1) heterosis for number of nodes up to primary raceme, total length of primary raceme and effective length of primary raceme in both the crosses, JM-6 x 48-1 and JI-436 x PCS-124; for days to flowering of primary raceme in JI-436 x PCS-124 over better parent; for days to maturity of primary raceme in JM-6 x

48-1 over better parent and in cross JI-436 x PCS-124 over mid parent; for plant height up to primary raceme in both the crosses over mid parent and in JM-6 x 48-1 over better parent; for number of effective branches per plant in both the crosses over better parent and over mid parent in JM-6 x 48-1; for number of capsules on primary raceme in both the crosses over better parent and over mid parent in JI-436 x PCS-124; for shelling out turn in both crosses over mid parent and over better parent in JM-6 x 48-1; for 100-seed weight in JM-6 x 48-1 over mid parent and over better parent; for seed yield per plant in JI-436 x PCS-124 over mid parent and over better parent; for oil content in JM-6 x 48-1 over mid parent and over better parent.

On the other hand, the observed heterosis either significant or non-significant showed a close agreement to expected (2) heterosis for seed yield per plant in JM-6 x 48-1 over better parent and for oil content in JM-6 x 48-1 over better parent, which indicated that the estimation of genetic parameters, on which the expected heterosis was based, has been carried out using most appropriate model. Discrepancy observed between actual and expected relative heterosis and heterobeltiosis in the above cases might be due to involvement of higher order interaction and/or presence of linkage. According to Mather and Jinks (1980) [11], if heterosis is measured on which an additive-dominance model is adequate, the positive and negative heterosis can occur only when [h] is greater than [d]. For this [h] must be greater than [d] for some or all genes, that is there must be super dominance or over dominance at some or all the loci. Secondly there must be dispersion of completely or incompletely dominant genes. Unfortunately neither degree of dominance nor degree of association can be estimated from generation means. The distinction between these two causes of heterosis cannot be made without recourse to second degree statistics *viz*., variance and covariance.

If the heterosis is measured both on digenic or trigenic interaction model, its specification becomes more complex and there are many ways in which heterosis could arise. Nevertheless, it is more likely to arise with a greater magnitude when [h], [l] and [z] have the same sign, that is, interaction is predominantly of a complementary kind as well as the interacting pairs of genes are dispersed so that their contribution to the degree of association is either very small or zero and hence their contribution to [d], [i] and [w] is negligible. In the present study, the presence of duplicate type of epistasis, whenever found in the experiment as a whole, support the magnitude of observed heterosis for most of the characters recorded in both the crosses. Though linkage does not affect the specification of the parental and F_1 means, it bias the estimates of three of the four components of heterosis *viz*., [h], [i] and [l] for digenic interaction and five of the six components of heterosis *viz*., [h], [i], [l], [w] and [z]. So if linkage is present, it will distort the relative magnitude of these components and affect the interpretation of the causes of heterosis. There was digenic linkage, for many traits affect both the crosses due to significance of [pi], [p^2i], [pj], [p^2j] and all four [pl] gene effects in the present study. The observed heterosis was found to have resulted either due to the action of dominance component only or due to the combinations with either trigenic or linked digenic types of epistasis for different characters in two crosses of castor. In most of the cases, the observed heterosis was either due to dominance [h], dominance x dominance [l] interaction and dominance x dominance x dominance [z] interaction or only due to dominance [h] effect or dominance x dominance [l] or dominance x dominance x dominance [z] interactions especially in the case where trigenic model was adequate.

High inbreeding depression for seed yield and its component traits is undesirable in castor crop as vigour decline from generation to generation and delay the development of inbred lines. The estimates for inbreeding depression was found significant but negative for days to flowering of primary raceme, days to maturity of primary raceme and number of effective branches per plant in cross JM-6 x 48-1; for plant height up to primary raceme and 100-seed weight in JI-436 x PCS-124 and for shelling out turn in both the crosses (Table 1).

Significant and positive inbreeding depression was observed for number of nodes up to primary raceme, total length of primary raceme, effective length of primary raceme, 100-seed weight and seed yield per plant in cross JM-6 x 48-1; for days to maturity of primary raceme and number of effective branches per plant in cross JI-436 x PCS-124 and for number of capsules on primary raceme and oil content in both the crosses.

The significant and positive inbreeding depression was reported by Pathak *et al.* (1988) [17] for 100-seed weight and seed yield per plant; by Singh *et al.* (2013) [20] for days to maturity of primary raceme, plant height up to primary raceme, number of nodes up to primary raceme, total length of primary raceme, effective length of primary raceme, number of capsules on primary raceme, 100-seed weight, seed yield per plant and oil content; by Barad *et al.* (2019) [3] for total length of primary raceme, effective length of primary raceme, number of capsules on primary raceme and 100-seed weight; by Mori (2019) [13] for days to flowering of primary raceme, plant height up to primary raceme and number of nodes up to primary raceme, total length of primary raceme, effective length of primary raceme, 100-seed weight and oil content and by Movaliya (2020) [14] for plant height up to primary raceme, number of nodes up to primary raceme, total length of primary raceme, number of capsules on primary raceme, 100-seed weight, seed yield per plant and oil content, which supports the results obtained in the present study.

The observed inbreeding depression was quite close to expected (1) values in cross JM-6 x 48-1 for number of nodes up to primary raceme, shelling out turn and 100-seed weight and in cross JI-436 x PCS-124 for total length of primary raceme and oil content showing fitting of trigenic interaction model. While the observed inbreeding depression was quite close to expected (2) values in cross JM-6 x 48-1 for days to maturity of primary raceme, plant height up to primary raceme, number of effective branches per plant and oil content revealing fitting of linked digenic interaction model.

Conclusion

It could be concluded from the present study that cross JM-6 x 48-1 had high and significant relative heterosis and heterobeltiosis for seed yield per plant and its component traits *viz*., total length of primary raceme, effective length of primary raceme, shelling out turn, 100-seed weight and oil content. Moderate inbreeding depression was observed in the present study as a whole. Therefore heterosis breeding is fully exploited in castor for genetic improvement in term of seed yield and its components. More over there was close agreement between observed and expected (1) heterosis over mid and better parent revealed that trigenic parameter model was more fit for most of the characters in both the crosses. Biparental mating could be followed which would facilitate exploitation of both additive and non-additive gene effects simultaneously for genetic improvement of seed yield and its component traits in castor.

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